

RESEARCH ARTICLE

Isotopic Niche Variation in a Higher Trophic Level Ectotherm: Highlighting the Role of Succulent Plants in Desert Food Webs

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Abstract

Stable isotope analysis of animal tissues allows description of isotopic niches, whose axes in an n-dimensional space are the isotopic ratios, compared to a standard, of different isotope systems (e.g. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$). Isotopic niches are informative about where an animal, population or species lives and about what it consumes. Here we describe inter- and intra-population isotopic niche (bidimensional $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space) of the Orange-throated whiptail (*Aspidoscelis hyperythra*), an arthropodivorous small lizard, in ten localities of Baja California Sur (Mexico). These localities range from extreme arid to subtropical conditions. Between 13 and 20 individuals were sampled at each locality and 1 cm of tail-tip was collected for isotope analysis. As expected, interpopulation niche width variation was much larger than intrapopulation one. Besides, isotopic variation was not related to age, sex or individual size of lizards. This suggests geographic variation of the isotopic niche was related to changes in the basal resources that fuel the trophic web at each locality. The position of Bayesian isotope ellipses in the δ -space indicated that whiptails in more arid localities were enriched in ^{13}C , suggesting most of the carbon they ingested came from CAM succulent plants (cacti, agaves) and in minor degree in C_4 grasses. Contrarily, whiptails in subtropical areas were depleted in ^{13}C , as they received more carbon from C_3 scrubs and trees. Localities closer to sea-level tended to be enriched in ^{15}N , but a clear influence of marine subsidies was detected only at individual level. The study contributes to identify the origin and pathways through which energy flows across the trophic webs of North American deserts.

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Introduction

The classical concept of ecological niche corresponds to a hypervolume in n-dimensional space, with the axes representing environmental variables (or resources) along which it is delimited the range where a species can survive (fundamental niche) or actually is present (realized niche) [1–2]. But historically practical difficulties to apply the niche concept to different species and circumstances [3] moved some ecologists to accept that, although the "niche is a central concept of ecology (. . .) we do not know exactly what it means" [4], reaching some of them (e.g. [5]) to recommend avoid the term niche in the scientific literature.

Recently, however, new methodological and technological approaches are renewing the concept of ecological niche and improving the ways to quantify it [6–7]. In particular, the use of stable isotope analysis (hereafter, SIA) on animal tissues is allowing describing isotopic niches, whose axes in a multidimensional space would be different isotopic signatures (e.g. $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) [8]. Isotopic values can indicate what an animal had consumed (e.g. [9]) and some characteristics of the place or the habitat in which it lives or lived (e.g. [10]).

Isotopic signatures of primary producers are carried up to the highest levels in the food web with only minor changes. Thus, the geographic variation in the isotopic niche of generalist predators would reflect spatial changes in their food-webs [11]. For example, intraspecific variation in isotopic niche has been detected between predator populations of distant areas [12] and those relying on freshwater and marine food-webs [8]. At lower spatial scales, isotopic niche of particular populations will include individual variation in the ranges of prey consumed, but also intra-locality variation among food sources [13–14]. Consequently, interpopulation variation in isotopic niche across a species range can inform about the spatial patterns of isotopic variation in primary producers, while within-population variation can illustrate about individual patterns of resource use at local level.

We have compared the long-term isotopic niche of ten populations of Orange-throated whiptail (*Aspidoscelis hyperythra*; Sauria, Teiidae). *A. hyperythra* is an arthropodivorous small lizard that can be considered a good model of higher trophic-level consumer at the Baja California desert food-webs (see below). We used estimates of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in body tissues characterized by a low-turnover. Our main aim was to relate whiptail niche variation to geographic differences in the type of plants fuelling the communities and to individual (intrapopulation) variability in the use of resources.

The main condition to obtain informative results from SIA is to have enough variation in the isotopic composition of the primary resources [6]. In our study, we expected to find at least four sources of isotopic variation: a) at interpopulation scale, primary producers at different areas would be mainly succulent plants (many cacti and some agaves) or bushes and trees; both groups use different photosynthetic pathways and consequently their $\delta^{13}\text{C}$ signatures are very different (see [Methods](#) and [S1 Table](#)); b) also, the food-webs of the areas closer to the sea could be more or less subsidized by nutrients from marine origin, which have contrasting $\delta^{15}\text{N}$ signatures [15]; c) at intrapopulation scale, individuals can behave as specialist on different food sources at isotopic level ("individual niche") [16]; for instance, home ranges of individual lizards vary in vegetation, soil type, humidity, etc.; this will make some individuals to rely more on arthropods feeding on succulents, while others will rely on those feeding on bushes; d) finally, at the localities with less complex communities it could be expected to find shorter food-chains, which could be detected at the isotopic composition of predators (mainly $\delta^{15}\text{N}$, that increases about 3 points upwards each trophic level [17–18]; however, this discrimination factor could be lesser in ectotherms, making difficult the assignation of trophic levels [19–20]). Based on these potential sources of variation we predict:

1. Interpopulation variation in the isotopic niche of our high-level predator will be greater than intrapopulation variation, mainly (but not only) due to the contrasting vegetation characteristics in our sampled localities.
2. The isotopic niche of each population will reflect the biotic and abiotic environmental conditions of the area. An increased importance of succulents as primary producers fuelling the food-web, detected as an enrichment of ^{13}C (i.e. less-negative values of $\delta^{13}\text{C}$) and maybe higher $\delta^{15}\text{N}$, was expected at drier, more desert localities. Also, the probability of detect some influence of marine subsidies through an enrichment of ^{15}N , should be higher at low altitudes and closer to the sea.
3. Individual (intrapopulation) variation in the isotopic niche should be high, as whiptails have reduced home ranges and thus each of them is dependent on the resources of a limited area in the “mosaic nature of the environment” [1]. Thus, they could behave as specialist although the species or population was generalist [14, 21]. However, we do not expect isotopic variation related to the sex or size of lizards, because they are very generalist arthropodivores, lack of apparent sexual dimorphism and use the same habitats all along their life (see below).

Until now, few studies have used small terrestrial ectotherms as model organisms for isotopic studies (but see [22–24]). Also, SIA have been relatively scarce in desert biomes [25]. To our knowledge, this is the first study evaluating geographical variation in the isotopic niche of a desert high-trophic level ectotherm. The results should be informative about the less-known relative importance of different plant types as producers fuelling animal communities in North American deserts.

Study System, Material and Methods

Model species

Orange-throated whiptails (herein whiptails) are small lizards (4–7 g in weight) native to Southwestern California (USA) and the peninsula and some islands of Baja California (Mexico). Their sexual dimorphism is scarce, being not possible to distinguish males from females at field conditions unless you catch them. They are non-territorial and forage actively during the day, searching in the leaf litter, the shallow soil and the low branches for a large variety of animal foods ([26–30], authors pers.obs.). Following [31], they should be considered generalist arthropodivores. Their individual hunting range is small, about 445 m² [32], while the mean distance between recaptures of the same individual approached 11 m [28]. Because of their foraging behaviour (they are active searchers and not ambushers [30]) and their wide food-spectrum, they can be considered suitable “samplers” of the local community of arthropods, which includes different trophic roles (herbivores, detritivores, predators, parasitoids). Therefore, the species is a good model of higher-level consumer in the desert community.

Study area

The study has been carried out in the southernmost quarter of the Baja California peninsula, approximately between 23°N–26°N in latitude and 109°W–112°W in longitude. Baja California is a volcanic fringe of land running from north-west to south-east, 1300 km long and, on the average, about 100 km wide. Most of the study area is considered “thermotropical” [33], with annual mean temperature of about 23°C. Rains, concentrated mainly in the summer, are very scarce, increasing towards the south and in altitude (we did not sampled whiptails above 500 m; see Table 1 for characteristics of each locality).

Table 1. Main characteristics of the ten sampled localities (ordered from South to North).

Locality	Coord. (N, W)	Coastline dist. (km)	Altitude (m.a.s.l)	Rainfall (mm)	Veget.type	$\delta^{13}\text{C}\text{‰}(\text{n})$	$\delta^{15}\text{N}\text{‰}(\text{n})$
CSL	22.92360109.9774	4.22	173	239	1	-17.87 ± 0.36 (16)	10.32 ± 0.26 (16)
MIG	23.06735110.0984	0.98	45	202	2	-21.29 ± 0.32 (19)	11.16 ± 0.33 (19)
CNAR	23.24340109.7461	21.74	209	413	1	-25.22 ± 0.70 (19)	10.73 ± 0.13 (20)
RIB	23.56870109.5598	2.72	27	217	1	-20.33 ± 0.14 (20)	12.81 ± 0.48 (20)
BART	23.74020109.8694	15.97	447	397	1	-21.89 ± 0.13 (19)	7.83 ± 0.27 (19)
INO	23.77415110.6611	1.98	13	93	4	-17.89 ± 0.27 (19)	14.31 ± 0.21 (19)
KM 83	24.26863110.9555	19.69	153	129	2	-18.26 ± 0.33 (20)	12.58 ± 0.21 (20)
TECO	24.34629110.2862	0.53	31	217	3	-18.47 ± 0.39 (15)	7.74 ± 0.30 (17)
IHU	24.97434111.4075	51.63	134	160	2	-17.03 ± 0.43 (13)	12.09 ± 0.40 (13)
BAJO	26.08441111.3253	0.09	8	130	2	-21.53 ± 0.28 (20)	13.13 ± 0.34 (20)

Sample sizes (n) and levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean ± SE) correspond to lizard tail tips for each locality. Shortest distance to the coastline and average altitude were obtained from a GIS of the area, average annual rainfall was estimated from WORLDCLIM Ver. 1.2 (<http://www.worldclim.org>) and vegetation type was assigned from 1:250000 charts of [77]. Vegetation types: 1, deciduous dry forest; 2, desert scrubs (mostly Cactaceae); 3, halophyte scrubs; 4, fog desert shrub (mostly Cactaceae, but with humidity from the sea and lichens).

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Very arid desert conditions predominate in the north of the area, while subtropical conditions influence the south [34]. Many species of cacti are present in the desert, especially giant cardons (*Pachycereus pringlei*), which frequently characterize the landscape, and *Opuntia* spp., *Stenocereus* spp., *Ferocactus* spp., *Mammillaria* spp., etc.; different agaves (*Agave* spp.) and Joshua trees (*Yucca* spp.) are common too; trees are scarce (some legume trees such as *Prosopis* sp. and *Lysiloma candida* at the usually dry riverbeds) but there are shrubs, such as *Larrea divaricata* and *Fouquieria* spp. On the other hand, at the subtropical thorny forest of the south, succulents are also abundant, mainly at low altitude, but woody shrubs, large bushes and deciduous trees, including *Bursera* spp., *Lysiloma divaricata*, *Tecoma stans*, *Cyrtocarpa edulis*, *Jatropha cinerea*, *Cercidium* spp., *Caesalpinia* spp., *Mimosa xantii*, etc., predominate [35]. Near the shore there are some mangrove species (*Rhizophora mangle*, *Laguncularia racemosa*, *Avicennia germinans*).

Succulents, trees, shrubs and grasses use several photosynthetic pathways, which have an important effect on their isotopic signatures [36]: C_3 plants fix CO_2 using the enzyme ribulose biphosphate carboxylase and typically have $\delta^{13}\text{C}$ values rounding -28‰ (-26.43 ± 1.75, mean ± SD, in our samples; S1 Table); C_4 plants take up initially CO_2 by carboxylation of phosphoenolpyruvate, having $\delta^{13}\text{C}$ signatures around -14‰ (-14.86 in our sample; S1 Table); CAM plants refer to Crassulacean Acid Metabolism and have $\delta^{13}\text{C}$ signatures rather similar to C_4 plants (-13.91 ± 1.24 in our sample; S1 Table). While cacti and agaves (and at least one succulent Euphorbiaceae species) are photosynthetic CAM plants in Baja California, trees are obligate C_3 and, according our data (see S1 Table), all woody shrubs would be C_3 plants. Most grasses are potential C_4 plants (S1 Table), but they are spatially and temporally very scarce in the area, except locally following summer rains, which do not reach all areas every year.

Whiptail capture and sampling

In different periods from September 2005 to February 2010, between 13 and 20 whiptails were captured and sampled in each of ten localities well-spaced in the area (Fig 1). These localities vary widely in vegetation type, annual rainfall, altitude and distance to the sea (see Table 1). To avoid killing whiptails, we snared them with nooses across their head, by a fishing rod with a thread loop at the tip. Immediately after capture, each individual was sampled by cutting about 1 cm of the tail tip using a scalpel disinfected with ethanol, and released within a few minutes, of

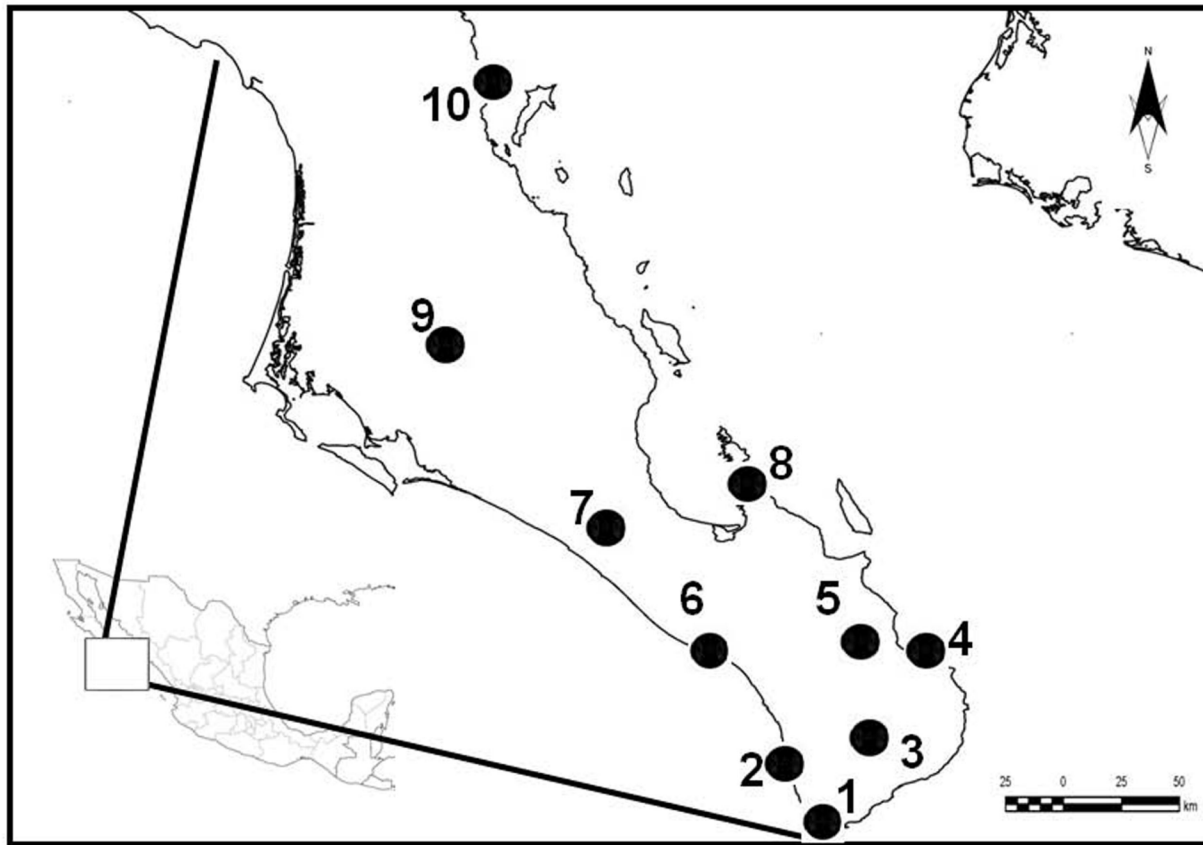


Fig 1. Map of the study area showing the sampled localities. 1: Cabo San Lucas (CSL). 2: Migriño (MIG). 3: Camino de los Naranjos (CNAR). 4: La Ribera (RIB). 5: San Bartolo (BART). 6: Los Inocentes (INO). 7: Kilómetro 83 (KM83). 8: El Tecolote (TECO). 9: Presa de Ihuazil (IHU). 10: El Bajo (BAJO).

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all them run immediately. Individuals with obviously regenerating tail were overlooked. Tail-clipping is frequently used in the study of reptiles, as it is considered a nondestructive sampling technique (e.g. [37]). Besides, at field conditions it is an efficient method for preventing re-sampling. Whiptails have the ability for tail autotomy and posterior regeneration, so the loss of just the tail tip should not be too stressful for them (see [38]). Tail tip clips were used for isotopic analyses.

All animals were captured on open public land and close to roads or villages, where free access and transit was allowed. Because the localities CNAR, MIG, BART and RIB are in the buffer zone of the Biosphere Reserve “Sierra de la Laguna” and *Aspidoscelis hyperythra* is an endemic species catalogued in Mexico as threatened, to obtain the permit from the authorities we send them previously a detailed protocol. Permission for the complete protocol (capture, sampling of tail, and releasing) was obtained from the environmental authority in Mexico (D.G. Vida Silvestre, Secretaría de Medio Ambiente y Recursos Naturales, México, permit # 11311; see Acknowledgments section), who is in charge of the ethical considerations. There is not a formal Institutional Animal Care and Use Committee.

Stable isotopic analyses

Isotope measurements were carried out at the Stable Isotope Laboratory of the Instituto Andaluz de Ciencias de la Tierra (CSIC-UGR, Granada, Spain). Organic matter (lizard tail tips and plant tissues) was homogenized and later analyzed for the isotopic composition of nitrogen

and carbon by means of a Carlo Elba NC1500 (Milan, Italy) elemental analyzer on line with a Delta Plus XL (ThermoQuest, Bremen, Germany) mass spectrometer (EA-IRMS). Because practically lizard tail tip does not contain lipids [39] and little is known in detail about isotopic routing in Lacertidae, we did not extract lipid from our samples (but see [40]). The stable composition of samples is reported as δ values per mil:

$$\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) * 1000$$

Where $R = 13C/12C$ for $\delta^{13}C$ values and $R = 15N/14N$ for $\delta^{15}N$ values.

Commercial CO_2 and N_2 were used as the internal standard for the carbon and nitrogen isotopic analyses. For carbon, two internal standards of -30.63 ‰ and -11.65 ‰ (Vienna Pee Dee Belemnite; VPDB) were analyzed every 10 samples. For nitrogen, two internal standards of -1.02 ‰ and +16.01 ‰ (AIR) were used. Precision calculated, after correction of the mass spectrometer daily drift, from standards systematically interspersed in analytical batches was better than $\pm 0.1\text{‰}$ for both $\delta^{13}C$ and $\delta^{15}N$.

All the individual isotopic values can be consulted in additional supporting data (S2 Table)

Isotopic niche metrics

Isotopic niche characteristics were described with quantitative metrics developed by [41], which used mean $\delta^{13}C$ and mean $\delta^{15}N$ of all species in a given community. In order to adapt their community level metrics to a population level, able to encompass intra and interpopulation variation, we did not use means, but the values of $\delta^{13}C$ and $\delta^{15}N$ of all individuals sampled in each population. For each population we calculated:

1. Total Area (TA) of the convex hull encompassing all points, which can be considered a measure of population niche width. Nevertheless, because this estimator is very dependent of sample size (e.g. [42]), we also calculated:
2. Bayesian Standard Ellipse Area (SEA_B), bootstrapping data ($n = 10000$). Standard ellipse (SEA) contains approximately 40% of the points and it is a measure of the mean core population niche, being to bivariate data as standard deviation is to univariate data [43]. It provides a good estimate of the population niche area, but with tendency to underestimate at small size samples. SEA_B nullify this bias, allowing comparisons among populations widely differing in size sample. Mean areas and the low and upper 95% credible limits will be shown. Additionally, we calculated:
3. Carbon range (CR) and Nitrogen range (NR), corresponding to the distance between the two individuals with the highest and the lowest $\delta^{13}C$ and $\delta^{15}N$ values within each population; they estimate the total carbon and nitrogen range exploited by each population.
4. Mean Distance to Centroid (CD), calculated as the mean Euclidean distance of each individual of a population to the $\delta^{13}C$ - $\delta^{15}N$ centroid for that population; it is an estimator of the population isotopic diversity.
5. Mean Nearest Neighbor Distance (MNND) that reflects the packing of the individuals in the two-dimensional isotopic space.

All calculations were made in R using the SIAR package [44].

Geographic variation analysis

Besides the graphical representation of the ellipses characterizing isotopic niches, differences among localities in $\delta^{13}C$ and $\delta^{15}N$ levels were analyzed fitting general linear mixed models

using Proc Glimmix in SAS [45], including the sampling date as a random factor. To evaluate our prediction that $\delta^{13}\text{C}$ local levels would relate to aridity and those of $\delta^{15}\text{N}$ to coastline distance, altitude, and aridity, we regressed their mean values across localities. In addition to evaluating our predictions, we also evaluated the effect of other five ecological correlates or potentially confounding factors: season (i.e. proportion of individuals sampled in summer-autumn), age (proportion of sampled adults), sex (proportion of adult females when juveniles were not considered), size (snout-vent length) and occurrence of regenerated tail (proportion of sampled individuals with apparently regenerated tail). Because of departures from normality and the presence of outliers, we used robust regression [46] rather than least-squares regression. Robust fits are minimally influenced by outliers in the independent variable space, in the response space, or in both. Analyses were performed by using robust MM-regression procedure available in S-Plus 6 [47], and the significance of each variable was assessed by using robust F-tests (F_R).

Given that spatial autocorrelation could inflate Type I statistical error, we evaluated whether residuals from significant robust fits for mean population values were spatially autocorrelated. To this end, we used Moran's I mark-correlation function [48] which allowed us to investigate how the residuals of two populations separated by distance r differ from their expected value under a null model of not spatial autocorrelation. It ranges from -1 (indicating perfect dispersion) to $+1$ (perfect correlation). Spatial autocorrelation analyses were conducted with the software *Programita* [48] available at www.Programita.com.

Results

Isotopic niche descriptors

Our localities differ widely in biotic and abiotic conditions, as well as in the average isotopic values of their whiptail tissues (Table 1). Also, there is a substantial geographic variation in the isotopic metrics (Table 2) and the position of population ellipses in the bi-dimensional $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space (Fig 2).

As expected, niche area was much broader at the species than at the population level, both for Total Area (TA) and for Bayesian Standard Ellipse Area (SEA_B) (Table 2). Specifically, SEA_B at the species level was, on average, five times larger than at the population level, and up

Table 2. Stable isotope niche metrics for each lizard population and the whole sample.

Populations	TA	SEA_B (95% limits)	CR	NR	CD	MNND	n
CSL	11.15	4.40 (4.38–4.42)	5.36	3.53	1.51	0.64	16
MIG	17.42	6.26 (6.23–6.29)	5.93	5.47	1.73	0.63	19
CNAR	12.96	6.35 (6.32–6.38)	8.52	2.01	2.75	0.62	19
RIB	13.08	4.71 (4.69–4.73)	2.71	7.26	1.70	0.44	20
BART	4.69	2.09 (2.08–2.10)	2.78	4.45	1.03	0.30	19
INO	10.13	3.63 (3.61–3.64)	6.51	2.77	1.14	0.54	19
KM 83	12.74	4.50 (4.48–4.52)	6.51	3.68	1.41	0.66	20
TECO	13.22	5.78 (5.75–5.81)	4.68	3.64	1.72	0.76	15
IHU	19.28	7.58 (7.54–7.62)	6.29	4.66	1.92	1.01	13
BAJO	18.66	5.76 (5.75–5.79)	5.19	6.88	1.57	0.70	20
TOTAL	112.0	21.03 (20.99–21.06)	14.2	12.1	3.28	0.39	180

TA = Total area of convex hull; SEA_B = Bayesian standard ellipse area; CR = $\delta^{13}\text{C}$ range; NR = $\delta^{15}\text{N}$ range; CD = Mean distance to centroid; MNND = Mean nearest neighbour distance; n = bivariate sample size.

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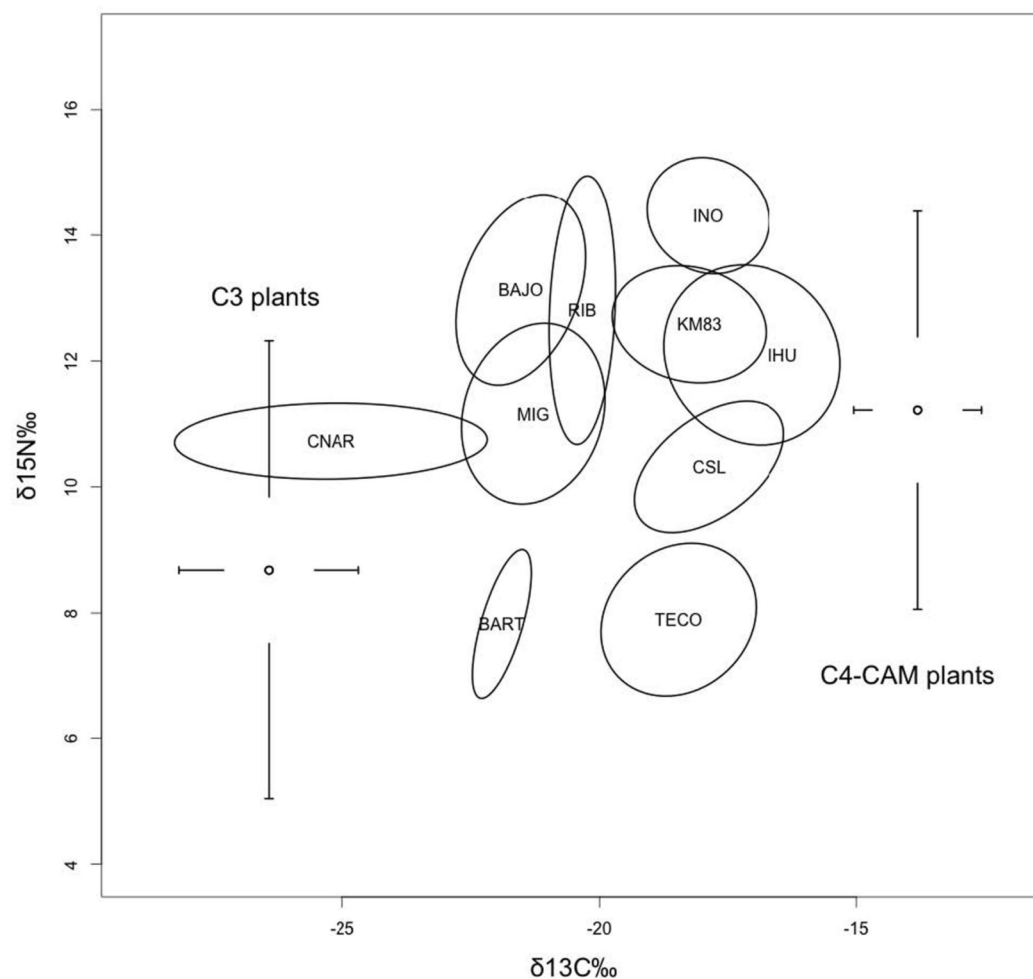


Fig 2. Stable isotope standard ellipses of whiptails for each of ten studied localities in southern Baja California (Mexico). Ranges and mean values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of C_3 y C_4 -CAM plants sampled in the whole area are also shown. Localities are named according to Table 1.

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to ten times larger as compared with the smallest population value (BART). That suggests the wide whiptail species isotopic niche results in fact from the sum of thinner, more specialized, local niches. At population level, large niches as estimated by TA (e.g. IHU, MIG) seemed to be more related to simultaneously high values in Carbon Range (CR) and Nitrogen Range (NR) than to extreme values in any of them (e.g. CNAR, RIB).

Considering all individuals, CR and NR were rather large, indicating that whiptails use a large range of isotopic resources. $\delta^{13}\text{C}$ ranged from -28.67‰ to -14.44‰ (coefficient of variation [CV] = 14.1%), encompassing the whole range of the plants sampled in the area (in fact, some vegetal source in CNAR, at least, must be more depleted in $\delta^{13}\text{C}$ than any of the plant species represented in S1 Table). $\delta^{15}\text{N}$ ranged between 5.7‰ and 17.8‰ (CV = 21.6%), inside the range of plants (C_3 plants, mean \pm SD = 8.68 ± 3.64 ; C_4 -CAM plants, 11.22 ± 3.16). CR and NR varied widely among populations. The highest CR corresponded to CNAR, just the population more depleted in ^{13}C on the average. Also, the highest NR corresponded to RIB, the second population more enriched on the average in $\delta^{15}\text{N}$.

Although not precisely, at population level, the metrics related to isotopic diversity (Mean Distance to Centroid, CD) and packaging (Mean Nearest Neighbor Distance, MNND) were

related to estimators of niche width. For instance, the highest CD corresponded to CNAR, the population having a largest CR, and the lowest one to BART, the population having smallest TA, SEA_B and MNND. Also, the highest MNND corresponded to IHU, the population having largest TA and SEA_B.

With respect to the position of the ellipses in relation to $\delta^{13}\text{C}$ axis (Fig 2), CNAR ellipse had the lowest central value (-25.22), while the more enriched was IHU ellipse (-17.03). En relation to $\delta^{15}\text{N}$, the lowest central value corresponded to TECO population (7.74) and the highest to INO (14.31). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ tended to be positively related (see below).

Geographical variation

We did not find any relationship of $\delta^{15}\text{N}$ with non-geographical factors such as sampling season, age, sex, size, or the occurrence of a regenerated tail ($P > 0.166$; see Table 3). In the case of $\delta^{13}\text{C}$, sampling season, age, size, or the occurrence of a regenerated tail did not have any significant effect ($P > 0.074$; Table 3). However, $\delta^{13}\text{C}$ was negatively related with the proportion of females in population samples ($P < 0.001$; Fig 3E). This effect, again, was not revealed by standard least-square regression ($F_{1,8} = 0.096$, $P = 0.419$).

Contrarily, whiptails in the studied localities strongly differed in $\delta^{13}\text{C}$ value ($F_{9,163} = 34.65$, $P < 0.0001$). Average local values of $\delta^{13}\text{C}$ tended to be higher in more desert areas, i.e. there was a significant negative correlation between average $\delta^{13}\text{C}$ in each locality and annual average rainfall ($F_R = 4.72$, d.f. = 1, $P < 0.05$; Fig 3A). We also found strong differences in $\delta^{15}\text{N}$ among localities ($F_{9,165} = 62.17$, $P < 0.0001$). There was a significant negative relationship between local elevations and $\delta^{15}\text{N}$ average values ($F_R = 11.97$, d.f. = 1, $P < 0.001$; Fig 3B), suggesting that lizards living closer to sea level (RIB, BAJO, INO) tended to include a higher proportion of heavier N in their tissues. Interestingly, this relationship turned no-significant ($F_{1,8} = 3.57$, $P = 0.096$) when using standard least-squared regression, likely because in contrast with robust regression it does not account for the effect of outliers such as the locality TECO (Fig 3B). Indeed, this locality shows the lowest $\delta^{15}\text{N}$ value, although it is located close to the sea (also, it was the only one with halophyte vegetation; Table 1).

As expected, average $\delta^{15}\text{N}$ values were negatively related to average annual rainfall ($F_R = 11.43$, d.f. = 1, $P < 0.001$; Fig 3C), suggesting that increased local aridity enhanced $\delta^{15}\text{N}$ levels (INO, IHU, Km 83). Contrary to expectations, no relationship was found between local levels of $\delta^{15}\text{N}$ and distance to coastline ($P = 0.959$).

There was not any significant relationship between average values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across localities ($F_R = 0.32$, d.f. = 1, $P = 0.564$). However, when considering individual whiptails as

Table 3. Main results from robust regressions for the relationships of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in *Aspidoscelis hyperythra* tissue and different ecological correlates.

	$\delta^{15}\text{N}$			$\delta^{13}\text{C}$		
	d.f.	F_R	P	d.f.	F_R	P
Season	1	1.405	0.225	1	1.871	0.161
Age	1	0.166	0.676	1	1.250	0.252
Sex	1	0.002	0.967	1	13.19	0.001
SVL	1	0.065	0.794	1	0.327	0.558
Regenerated tail	1	1.830	0.166	1	3.033	0.074

Season: proportion of individuals sampled in summer; Age: proportion of sampled adults; Sex: proportion of adult females when juveniles were not considered; SVL, Snout-vent length; Regenerated tail: proportion of sampled individuals with clear sign of regenerated tail. Significant result ($P < 0.05$) in boldface.

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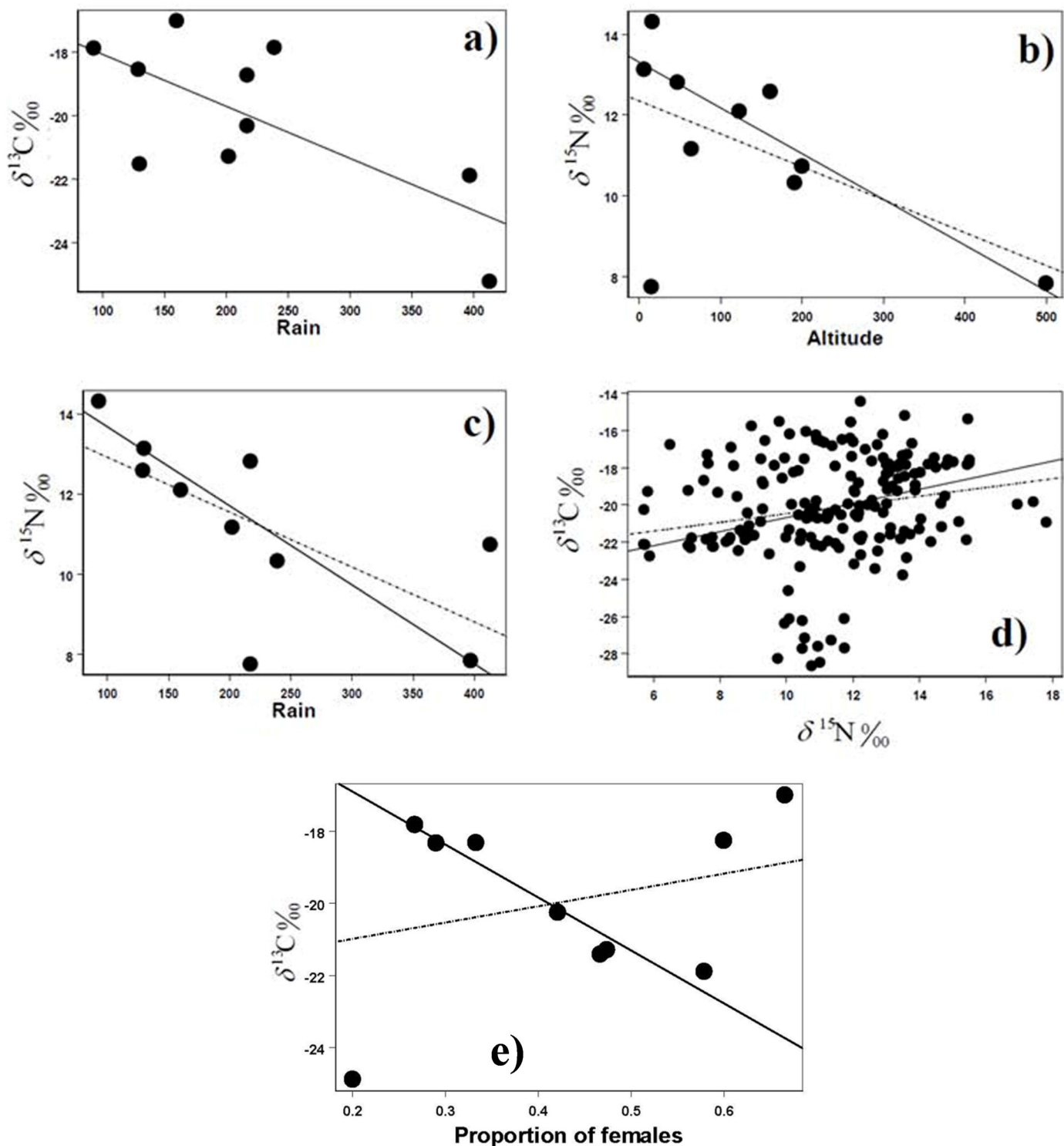


Fig 3. Relationships between isotopic values and several variables across the ten sampled localities in southern Baja California (Mexico). (A) Negative relationship between average values of $\delta^{13}\text{C}$ (a) or $\delta^{15}\text{N}$ (c) in whiptail tissues and the estimated annual rainfall (B) Negative relationship between average $\delta^{15}\text{N}$ values and local altitude. (D) Positive relationship of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across individual lizards ($n = 180$). Note that robust regression (continuous line) often differs somewhat from least-squares regression (dotted line). The arrows in charts b and c point to TECO sampling site. (E) Negative relationship between average values of $\delta^{13}\text{C}$ in whiptail tissues and the proportion of females in the ten sampled localities. Note that robust regression (continuous line) has even different sign (i.e. negative) than that estimated by standard least-squares regression (i.e. positive; dotted line).

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sampling unit ($n = 180$), there was a significant positive linear relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($F_R = 5.47$, d.f. = 1, $P < 0.05$; Fig 3D).

To evaluate a potential spatial autocorrelation in our data, we calculated Moran's I at a range of spatial scales for the residuals of the three significant relationships concerning mean population values (i.e. $\delta^{15}\text{N}$ vs. rainfall, $\delta^{15}\text{N}$ vs. altitude, and $\delta^{13}\text{C}$ vs. rainfall; Fig 3). In the three cases, observed Moran's I values were always within the simulation envelopes (S1 Fig), indicating a lack of spatial autocorrelation in the residuals.

Discussion

Use of tail tip clips as samples

Tail tip clips from ectotherm vertebrates are frequently used as non-lethal sources of material for genetic (e.g. [49]), toxicological (e.g. [50]) and isotopic (e.g. [37,51]) studies. However, it must be considered that, besides diet, a large number of physiological, ecological and methodological factors generate variation in the isotopic signature of animal tissues [52, 25]. In particular, replacement rates of nutrient pools in each particular animal tissue do vary [53–54]. We have sampled the distal 1 cm of tail tip, which is made mainly by scales, skin, and bone, presumably tissues with low turnover; in addition, carbon incorporation rates in ectotherms are slower than those in endothermic vertebrates [55]. All this should minimize the effect of potential short-term variations in diet in our study (e.g. [24]). Lack of differences between pre- and post-summer whiptail samples in both $\delta^{13}\text{C}$ ($P = 0.378$) and $\delta^{15}\text{N}$ ($P = 0.083$) values supports this idea. However, some uncertainty regarding exact whiptail tail tip turnover time does exist, although it should not change our conclusions. Besides, in aquatic snakes it has been proved that scale clips and tail clips of the same individual do not differ substantially in isotopic composition ([56]). We assume tail tip stable isotope composition integrates the diet of whiptails along a time-span of several months.

The wide isotopic niche of Orange-throated whiptail

For all-data pooled, the values of metrics related to isotope niche width, such as TA , SEA_B , CR y NR , indicate a large niche area for the species. Practically the whole range of isotope variation in plants of the area was encompassed by CR and NR at species level, confirming Orange-throated whiptails are able to cope with a large variety of resources. However, as we expected, this large niche at the level of species seems to be due to the sum of smaller niches at population and subpopulation levels [7, 14].

Hutchinson [2] suggested the niche of a species has sceno-poetic and bionomic dimensions. The sceno-poetic axes refer mainly to the bioclimatic stage in which a species performs (i.e. where it lives), whereas the bionomic axes refer to the resources it uses (i.e. how it behaves). The distinction is particularly relevant in the analysis of isotopic niches, as isotopic signatures of resources otherwise similar change geographically [6]. Our results strongly suggest that the broad isotopic niche of *Aspidoscelis hyperythra* is mainly due to its sceno-poetic dimensions, i.e. to changes related to the large distribution range of the species. To begin, we have discarded a possible influence of most of non-geographical factors, such as season and whiptail size, age and length (although our results indicate that the specific sex composition of samples could bias results and thus caution is needed in interpreting trends from samples with different gender proportions).

Geographical variation in predator or competitor pressure could generate geographic changes into the realized isotopic niche of a species, as proved by [57]. However, the spectrum of predators and competitors of *Aspidoscelis hyperythra* must be rather similar in all our localities. Hence, we suspect the variation we found was most related to geographical changes in

plant communities. Reinforcing this idea is the fact that the position of the population ellipses in the isotopic δ space can be related in a predictable way to geographical and environmental factors affecting plants (see below).

Whiptails are high-level generalist consumers, depredating on phytophagous invertebrates such as termites and on predators such as spiders. Unfortunately, we have not isotope data for arthropods at each locality. Thus, we cannot transform the isotopic niche in a trophic niche (see [6]) by applying the mixing models frequently used in the literature (see revisions in [25, 54]). However, by analyzing the position of population ellipses in the δ space we can infer the relative importance in the trophic web of producers with different isotopic signatures. For instance, according our predictions more arid and drier localities showed enriched average $\delta^{13}\text{C}$ values, while subtropical localities showed depleted values. These results strongly suggests that in more desert localities (e.g., INO, KM83, IHU, TECO; Table 1, Fig 2) succulent plants and/or C_4 grasses contribute most of the carbon circulating in the trophic web, while in more humid localities (e.g., BAR, RIB, MIG; Table 1) carbon would come both from succulents and C_3 plants; only in CNAR, the locality receiving more rainfall, most of the carbon in the trophic web seemed to come from C_3 scrubs and trees (Table 1, Fig 2).

Variation in $\delta^{13}\text{C}$: the role of succulents in Baja California desert food webs

Isotopic signatures of C_4 and CAM plants are very similar, although on the average CAM plants were enriched in ^{15}N (S1 Table). Would be C_4 grasses or CAM succulents the plants supporting high-level consumers in our desert food webs? Perhaps because most previous studies in dry areas took place in grasslands, many authors usually ascribed the nutrients labelled by less negative $\delta^{13}\text{C}$ values to C_4 grasses, neglecting the potential role of succulents (e.g. [58–60, 24]). However, as stated by [61], cacti and agaves can reach high densities and relative biomass in North America arid areas (e.g. until ~56% of seasonal above-ground biomass [62]) and several studies unequivocally showed that heavier carbon used by some desert consumers derived almost exclusively from cacti [61, 63–64]. In our study area, several evidences suggest that most of the nutrients enriched in $\delta^{13}\text{C}$ had their origin in cacti rather than in C_4 grasses. Succulents are dominant at the landscape (the study area includes the region of North America with more Cactaceae [65]), ground among bushes is usually barren, and frequently we saw no grasses in many of our ten sampling localities (S2 Fig). Besides, cacti feed a lot of arthropods [66] and we captured many lizards while foraging around and under dead cacti. In fact, a study in different localities at the centre of our study area showed that whiptails foraged mainly under the tree *Jatropha cinerea* and the cacti *Stenocereus gummosus* and *Cylindropuntia cholla* [67]. Also, the high $\delta^{15}\text{N}$ values detected in the tissues of most whiptails seemed to be closer to those of succulents than to those of C_4 gramineae in the area (S1 Table). Thus, our study suggests, as previously suspected, that the production by succulents is essential for animal communities in the Baja California desert.

Variation in $\delta^{15}\text{N}$: Are there marine subsidies?

The interpretation of isotopic nitrogen levels in lizard tissues is more complicated, as many factors influence them [68–69, 18]. Variability of $\delta^{15}\text{N}$ in plants may be high, mainly due to soil nitrogen cycling and plant physiology (see S1 Table). Besides, $\delta^{15}\text{N}$ increases with the trophic level, and thus animals higher at the food chain tend to have higher $\delta^{15}\text{N}$ values. Also, body condition affects the levels of isotopic nitrogen, as $\delta^{15}\text{N}$ increases in starving animals [70] (but see [71]). Finally, at least in endotherms water stress does increase the proportion of $\delta^{15}\text{N}$ in animal tissues [72, 18].

However, most of these factors influencing $\delta^{15}\text{N}$ can be considered minor ones when compared with the influence of marine subsidies at the food web. For instance, working with *Uta stansburiana* (another arthropodivorous lizard) at the north of the Gulf of California, it was found that $\delta^{15}\text{N}$ reached about 28.8 ‰ in individuals captured on islands subsidized by seabird guano, 17.9 ‰ in those of coastal areas without birds, and only 13.0 ‰ in lizards of inland areas [15]. Considering these values and those of the plants at our study area (S1 Table), a clear influence of marine subsidies cannot be recognized in none of our localities. This was expected, because the area of marine influence is rather thin (about 50 m; [15]) and we extended our capture grounds several hundreds meters inland, with the exception of BAJO). However, we have found a significant relation between the average levels of $\delta^{15}\text{N}$ and the altitude above sea level (Fig 2), suggesting some marine influence would be possible at lower localities (via insects feeding on marine products landed by people, mainly shells and fish remains, or on shore wrack, or receiving dust and aerosols [73]).

Our results in relation to $\delta^{15}\text{N}$ could be also partially explained by the isotopic composition of plants and the effects of water stress on the nitrogen-isotope ratios in animal tissues. Thus, the negative relationship between $\delta^{15}\text{N}$ and average rain (Fig 3C) could be expected. Also, the positive weak linear relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across individuals (Fig 3D) had been previously found for different species of endotherms, including humans [74, 18], and across species guilds [75].

Intrapopulation isotopic variation

We have discarded an influence of age, size and other individual conditions. However, we have detected a rather high intra-local variation (individual niche [16, 76]) at least in some populations. This was reflected in the values of Total Area of the convex hull (TA), Carbon and Nitrogen ranges (CR and NR), Mean Distance to Centroid (CD) and other metrics (Table 2). We were not able to detect any general trend among localities, but it seems that the populations where more diversity of resources was expected (i.e. those having simultaneously high abundances of C_3 and CAM plants), were those showing larger variation. For example, CNAR is the population more influenced by subtropical C_3 plants and also it is the only locality covering more than 50% of the total CR (Table 2); high CR in CNAR can be explained because most (13 of 19; values not shown) whiptails were very depleted in $\delta^{13}\text{C}$, suggesting they relied on C_3 plants derived resources, while 6 individuals enriched in $\delta^{13}\text{C}$ apparently relied more on C_4 -CAM plants derived resources. In the same way, the two localities with higher variation in $\delta^{15}\text{N}$ (RIB and BAJO, each of them covering more than 50% of the total NR; Table 2) were those placed lowest on sea level, where some influence of marine subsidies would be possible; in RIB, 17 individual whiptails had $\delta^{15}\text{N}$ values under 13.0 ‰, but three others surpassed 17.0 ‰ (values not shown), suggesting this individuals had an atypical diet more influenced by the sea. This intralocality variation was predictable because microhabitat features (e.g. presence of a dead cardon or a C_3 tree, availability of fishermen waste, etc.) can influence severely the isotopic signatures of available arthropods and thus whiptails.

Concluding notes

This is the first study concerning the geographic variation in the isotopic composition of body tissues of a desert higher-level-trophic ectotherm. Trophic webs in North American desert ecosystems are rather complex [31], but using stable isotopes as technical tool and an arthropodivorous lizard as model, we showed that in Baja California Sur cacti and agaves (CAM plants), and likely to a lower extent C_4 grasses, have a large importance in the supply of nutrients to the higher levels of the food webs, particularly in the more arid localities. Instead, the contribution

of C_3 shrubs and trees was important in southern localities with more rain and subtropical vegetation. A clear influence of marine subsidies has not been detected in any locality. Our study contributes to identify the origin and pathways through which energy flows in desert ecosystems, revealing overlooked food resources (i.e. cacti) with potential chief effects on the structure and dynamic of animal populations.

Supporting Information

S1 Fig. Spatial autocorrelation (measured as Moran's I) for the residual of the three significant robust fits. A), $\delta^{15}N$ and rainfall; (B), $\delta^{15}N$ and altitude; (C), $\delta^{13}C$ and rainfall. (TIF)

S2 Fig. The study area and lizards. (A) Landscape at a subtropical shrubland in the Southern of the study area; (B) Landscape at the dry desert in the North of the study area, with abundance of succulents; (C) a Whiptail capturing an Orthoptera in the South; (D) a whiptail on the Northern desert. All the pictures by M. Delibes. (TIF)

S1 Table. Values of $\delta^{15}N$ and $\delta^{13}C$ in sampled C_3 , CAM and C_4 plants collected at different localities of the study area in southern Baja California (Mexico). (DOC)

S2 Table. Values of $\delta^{15}N$ and $\delta^{13}C$ in each individual lizard sampled. The identification label corresponds to each population. (XLS)

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Author Contributions

Conceived and designed the experiments: MD MCB AD. Performed the experiments: MD MCB LS. Analyzed the data: MD MCB JMF AG LS AD. Contributed reagents/materials/analysis tools: AG AD. Wrote the paper: MD MCB JMF AG LS AD.

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